

EVOLUTION

Putting the Pieces Together

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The completion of a jigsaw puzzle brings tremendous satisfaction; however, a few missing pieces lead to considerable frustration. Having the intended picture of a puzzle on the container contributes to the satisfaction (or the frustration). But what about a puzzle where there is no master picture to guide the reconstruction? How do you know if you have all the pieces? And what if the contours of some pieces are unclear, making it difficult to see how they fit together? Such is the lot of biologists attempting to explain key evolutionary transitions in the history of life.

Fins into Limbs is an exploration of a long-standing evolutionary puzzle associated with the origin of tetrapods and the vertebrate invasion of land. Brian Hall has assembled a

stellar array of contributors from various fields that represent the pieces necessary for a solution. The volume is handsomely executed and also timely. It collects a diverse body of recent research on fins and limbs emerging from evolutionary developmental biology (evo-devo), functional morphology, and paleontology, all of which have transformed our conception of what the fin-limb transition looked like. Instead of a lobe-finned fish hauling itself up onto the sand, we have a much different image of the evolutionary transformation (1). Recent papers that could not be incorporated into the volume have revealed new transitional fossils (2) and continued to augment our understanding of the molecular genetic mechanisms of limb development (3).

The volume's first part, Evolution, provides historical background on the fin-to-limb puzzle and paired appendage locomotion, as well as a phylogenetic context informed by paleontology. The origin of the autopodium (hand/foot)—encapsulated in Hall's pithy slogan "fins minus fin rays plus digits equal limbs"—is analyzed from an evo-devo perspective. In the second part, Development, an overview of fin and limb ontogeny is followed by treatments of chon-

drogenesis, osteogenesis, apoptosis, joint formation, postnatal growth, and regeneration. The third part, Transformation, addresses the subsequent fate of tetrapod limbs, including the appendicular skeleton of amphibians, digit and limb reduction in reptilians, mammalian limb diversity, and skeletal adaptations for flight, digging, and swimming. These later chapters are not pieces of the puzzle themselves as much as investigations of other evolutionary transitions of tetrapod appendages relevant to understanding how the different pieces fit together when explaining the origin of innovations.

Although the lengths of the contributions vary substantially, the more interesting variation lies in the styles they exhibit: anatomical, functional morphological, and molecular genetic. Very few chapters bring these considerations together, and even the contrast among cognate entries is striking. Chondrogenesis and osteogenesis in fins are treated in terms of histology, whereas the entry on limbs grants priority to molecular genetics. The influence of model organisms (zebrafish, chicken, and mouse), chosen for different scientific puzzles, such as isolating key processes underlying how an organism develops from embryo to adult, is also apparent. My favorite was the last chapter, by Matthew Vicaryous and Wendy Olson, on the curiosity of sesamoids and ossicles in the appendicular skeleton. The combination of a topic nearly untouched by other contributors and an explicit blending of the different styles makes it a gem.

Specialists will no doubt question particular interpretations within individual chapters but the book's significance lies in the overarching outlook on the fins-into-limbs puzzle. Attacking the thorny empirical and conceptual questions that compose this problem requires multiple disciplinary approaches, each with specialized concepts and methods. Sometimes this introduces potential communication difficulties (e.g., the developmental "mesomere" of vertebrate mesoderm and anatomical "mesomeres" in pectoral fins), and the substantial differences in terminology are on full display. But do we have all the disciplinary pieces to the puzzle? The vol-

ume lacks discussions from evolutionary genetics and (paleo)ecology, which encourages a complaint that evolution plays second fiddle to comparative development in it. Some might disagree with claims about the evolutionary process, such as patterns of genetic regulatory elements pointing "to changes in a region-specific regulatory sequence as being the mechanism for evolutionary change." As the editor acknowledges, this book is focused on skeletal elements, which is his area of expertise (4). Thus, musculature, innervation, vasculature, and other features are relegated to the background, although some of these missing pieces can be found elsewhere (5).

Knowing how the pieces fit together is a more difficult question. The contributors make little effort to integrate the research from different approaches. One author notes that "the challenge is to continually synthesize knowledge gained from multiple perspectives into an ever more refined understanding." In some cases, this synthesizing is studiously avoided, and at other points there is inadvertent stumbling over borrowed concepts. (An exception is Gunter Wagner and Hans Larsson's discussion of evolutionary novelties, with its explicit fusion of anatomy, phylogeny, development, and evolution.) But this is not the fault of the editor or contributors. It is symptomatic of the complex structure of biological knowledge. Multidisciplinary research on evolutionary problems may be essential, but the nature of its composition and functioning remains elusive.

Fins into Limbs serves as a necessary reference and a worthy guide to future research on this and other evolutionary transitions. It tells us what we know, what we don't know, and what we'd really like to know. Thus it points us in the direction of which pieces are required to solve the puzzle and reminds us of the pressing need to figure out how they all fit together.

References

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